COEVOLUTION OF GRASSES AND HERBIVORES

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ABSTRACT

The appearance of fossilized silica bodies derived from the leaf epidermis of grasses and of mammalian fossils having high-crowned teeth was nearly simultaneous in lower to middle Eocene strata of Patagonia, where these fossils are associated with dry land sediments that indicate the presence of savannas containing shrubs and traversed by rivers that provided mesic habitats. In North America, the earliest clearly identified grass fossils are stipoid fruits of lower Miocene age, while the oldest mammals having high-crowned teeth are rhinoceroses of Miocene age. The abundant stipoid fruits known from the Miocene and Pliocene Epochs in the central United States indicate that the earliest Miocene species were quite different from modern counterparts, but that early Pliocene species have modern counterparts in the pampas of South America. During the Pleistocene, stipoid grasses ceased to be dominant elements of North American grasslands, being replaced by grasses belonging to the tribes Chlorideae and Andropogoneae. This change was associated with the appearance of a drier, more continental climate and with the appearance of bison and sheep on the North American plains. The evolutionary significance of these coordinated changes is discussed.

A fundamental tenet of modern evolutionary theory is that, at least with respect to visible morphological and anatomical characteristics, rates of evolution reflect to a large degree rates of change through time in the nature of population-environment interactions (Dobzhansky et al., 1977). Rapid evolution is often associated with successful responses to rapid and complex changes in the environment. The environmental changes that stimulate most strongly rapid evolution involve both the physical and biotic environment. Often the changes in climate and similar physical factors trigger off changes in structure and behavior on the part of those organisms that have the most direct relationships with the external environment, and these in turn affect other organisms of a given community.

An excellent example of rapid evolution as a result of this complex web of physical and organismic changes is the evolution of grasses and the herbivorous mammals that depend upon them. Paleobotanists and vertebrate paleontologists from both North America and South America have now accumulated data that can be synthesized into an account of this coevolution which, though admittedly partial, is nevertheless highly convincing. The very different history of events occurring on these two continents, plus the remarkable synchrony on each continent between the evolution of grasses and mammalian herbivores shows clearly the close interdependence between the evolution of these two very different kinds of organisms.

THE KINDS OF EVIDENCE THAT ARE AVAILABLE

The most important kind of evidence from which the story can be pieced together is provided by the fossil record. Fortunately, this record is remarkably good in both North and South America, including remains of both grasses and mammals. The grass fossils that are the most diagnostic are fruits that clearly belong to the tribe Stipeae. The pioneering monograph of these fruits prepared by Elias (1942) has now been supplemented by more modern and thorough re-

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search on the part of Thomasson (1978a, 1978b, 1979). The remarkable features of these fossils are both their abundance and the details of cellular structure that can be seen in them. Moreover, in contrast to most other fossils of angiosperms, they reveal characters of form that are usually used by systematists dealing with their modern counterparts as diagnostic of species and genera.

Next in importance are fossilized bits of leaf epidermis. To my knowledge, the only definite fossils of this kind are those discovered by Litke (1968) in coal deposits of eastern Germany. In them, cell outlines are perfectly preserved, so that identification to tribe is unquestionable. They show that at least one tribe of the family, the Oryzeae, was already differentiated by the end of the Eocene Epoch.

Of a similar character, but harder to identify, are the much more abundant bits of organic silica known as opalines, that occur in some sediments. These microscopic particles are derived from epidermal cells of grasses that have become fully impregnated with silica. When well preserved, they are diagnostic of subfamilies, as shown by Prat (1932) and others. Most reports of these fossils are from sediments of Pliocene age, but much older examples, some of them dating from the middle or early Eocene, have been reported from Patagonia, South America (Frenguelli, 1930; Teruggi, 1955; Bertoldi de Pomar, 1971, 1972).

The pollen of Poaceae is highly distinctive as to the family, but of little value for the recognition of its subdivisions. It does not become abundant until the Miocene Epoch, when evidence from fruits and epidermal fragments indicates that the family was already fully differentiated. For this reason, palynological fossils are among the least valuable for reconstructing the evolutionary history of the family. Leaves that on the basis of superficial appearance have been assigned to the family and given such generic names as *Poacites* are even less helpful. Recent studies of some of them on the basis of microscopic cellular structure has shown that they belong to other families of monocotyledons (Litke, 1968).

The supreme value of fossils of mammalian herbivores lies in the fact that the parts that are most commonly preserved—teeth and hoofs—are highly diagnostic of both their morphological relationships and their mode of life. High-crowned (hypsodont) teeth having complex patterns of enamel evolved in response to pressures exerted by a diet of hard, siliceous leaves, particularly those of grasses. Long slender legs that terminate in hoofs made up of one or two much enlarged toes evolved in response to rapid running or leaping in country that was at least partly open and free of dense forests. Consequently, hypsodont teeth and well-developed hoofs can be expected to be associated with fossil remains of grasses that are adapted to open country. The frequent presence of this coexistence, or coadaptive syndrome, will become evident from the facts to be presented below.

Direct fossil evidence can be supplemented by indirect evidence of several kinds. Particularly useful is that derived from detailed studies of sediments (Pascual & Odreman, 1971; Andreis, 1972; Spaletti & Mazzoni, 1978). The presence of saline deposits and gypsum in beds that are clearly terrestrial rather than marine in origin indicates at least seasonal drought. Other characteristics, such as deposits resulting from showers of volcanic ash, and the nature of indications of animal activity, such as burrows of worms and nests of scarab beetles, can also be helpful.

Another kind of indirect evidence can be obtained from comparative studies of successions of fossils through time. Because of their high diagnostic value, mammalian fossils are particularly helpful for deciding when a succession represents progressive evolution in situ, and when a change in faunas is due to migration from another region. Although successions of plant fossils are rarely complete enough to lead toward decisions of this kind, an exception is provided by the fruits of Poaceae, tribe Stipeae, that have been uncovered on the plains of the central United States. The combined study of these grass fossils and the mammalian remains associated with them provide the best opportunity for analyzing coevolution of terrestrial plants and animals over a long period of time that exists anywhere in the world.

Indirect evidence can also be obtained from geology, particularly the discipline of plate tectonics, that provides indications of past continental movements. This subject has been carefully reviewed by Raven & Axelrod (1974). Nevertheless, great caution must be used in applying this evidence to problems of plant and animal dispersal. Even with respect to organisms that are least able to be transported over long stretches of ocean, such as mammals, one cannot assume automatically that a land bridge is necessary to transport them from one continent to another. As reviewed by Patterson & Pascual (1968, 1972), a combination of comparative fossil evidence and that related to past continental movements indicates that during the end of the Cretaceous and the beginning of the Tertiary Period, several groups of mammals must have reached South America by migration over water. Since most seeds of angiosperms can be transported over long distances as easily or more easily than can mammals, the entrance of angiosperm groups into South America during the same period by occasional long distance migration can by no means be ruled out.

Finally, modern patterns of geographical distribution can supplement those provided by fossils. These must also be interpreted with caution, and associated with fossil distribution patterns whenever possible. With respect to grasses, the inference is reasonable that the migration of Stipeae, for which a fossil record is available, was accompanied by migrations of grasses belonging to other tribes, which left no record because both their vegetative parts and their seeds are too perishable. Since phylogenies involving polyploidy usually proceed from lower to higher levels (Stebbins, 1971, 1980) inferences about past patterns of distribution can often be obtained by comparing the distribution patterns of diploids and related polyploids (Stebbins, 1947, 1950, 1971).

RELEVANT FEATURES OF CLIMATIC CHANGE AND CONTINENTAL MOVEMENTS

The record of coevolution between grasses and herbivores spans most of the Tertiary and Quaternary Periods. It begins in southern South America (Patagonia) in the middle of the Eocene Epoch, about 45 million years ago, and continues until the retreat of the glaciers in the post-Pleistocene and the consequent post-glacial xerothermic stage permitted the establishment of open xeric grasslands in the west central part of the United States, plus adjacent Canada and Mexico, less than 10,000 years ago. Climatic and orogenic changes throughout this long period are relevant to the problem.

The story of these changes has been reviewed so many times that it does not need to be repeated here. North and South America underwent a gradual cooling of climate, accompanied by the rise of the western cordillera, that increased habitat diversity, and brought to the central regions of the continents the continental climate that now exists in them, characterized by cold winters and hot summers. Of particular interest, however, are the differences between the two continents in the intensity of these effects. The differences will therefore be reviewed.

In the first place, semiarid conditions, including the appearance of open savannas dotted with widely spaced trees and shrubs, appeared in South America about 20 million years before their appearance in North America. On both continents, the Paleocene Epoch was characterized by continuous forests perhaps interspersed by small enclaves of open country. In the middle of the Eocene, however, evidence from the Mustersan strata in the Province of Chubut, Argentina at 45° south latitude, indicates the presence of widespread savanna conditions, as is described in more detail below. Although direct evidence for the age of these strata is lacking, Marshall et al. (1977) have estimated their age as middle Eocene, about 48 million years old, on the basis of stratigraphic evidence plus a potassium-argon date of 35 million years for a sample from the younger Deseadan formation. At this time, evidence from the fossil record of both plants and animals indicates that central North America was still covered by more or less continuous forests.

Second, the greater land mass of North America caused that continent to respond to the uplift of mountains by acquiring a much greater degree of continentality than that which prevails in South America. This difference, which is evident to anyone who has travelled over the two continents, is clearly shown by comparisons between the different climate diagrams presented by Walter & Lieth (1967). Its relation to the timing of environmental changes is highly important. Equable climates persisted in central and eastern South America long after they had disappeared from corresponding parts of North America. This means that plant species or genera, arriving in South America during the Tertiary Period, had a greater change for persisting in a relatively unchanged condition than did their relatives that remained in North America. In many respects, the present, or rather pre-human conditions prevailing on the pampas of Argentina, Uruguay and southern Brazil during the Miocene and early Pliocene epochs probably resemble more the conditions that prevailed on the Great Plains of North America during the Miocene and early Pliocene epochs than those that prevail there today.

Another important difference is with respect to the biogeographic connections that existed on the two continents. South America was an island continent from the end of the Cretaceous Period until the end of the Tertiary. It received immigrations from other continents only via occasional long distance dispersal, except for a possible closer link with Antarctica. North America, on the other hand, was intermittently connected with Eurasia by land bridges that permitted extensive transmigrations of flora and fauna. Consequently, the early Tertiary mammalian fauna of South America was decidedly unbalanced, being derived from a few accidental introductions (Patterson & Pascual, 1972). Balance was achieved by extensive adaptive radiation from this small number of immigrant stocks. On the other hand, the fauna of North America was constantly receiving immigrants from Eurasia, so that the fauna of the Northern hemisphere was at

all times balanced, and contained several different potential competitors for each new ecological niche that was opened up as a result of environmental change. There is every reason for believing that the same factors produced comparable differences in the evolution of grasses and other angiosperms.

Finally, the two continents were affected very differently by the Pleistocene glaciation. In North America, the Great Plains, that during the Miocene and Pliocene epochs were the scene of coevolution of grasses and mammals, during the Pleistocene were ice covered over the northern part, and farther south became tundra, or coniferous forest (Davis, 1976). On the other hand, glaciation in South America was confined to the high Andes and the southern portion of Patagonia. The extensive grasslands that form the pampas of Argentina, Uruguay and southern Brazil were little affected by this change.

Three factors, therefore, would have contributed to the longer persistence and slower evolution of plains grasses in South America as compared to North America: (1) the longer persistence of equable climates in its temperate regions: (2) the lack of immigration and therefore of new levels of competition during most of the Tertiary Period: and (3) the comparatively mild influence of the Pleistocene glaciation. These factors were, however, balanced by another factor that greatly stimulated both evolution and extinction. This was the massive immigration of northern mammals into South America at the end of the Pliocene Epoch, as a result of the rise of the Panamanian land bridge. As is explained below, this immigration was most probably accompanied by a similar immigration of northern grasses and other angiospermous herbs.

THE SUCCESSION OF EVENTS IN THE TERTIARY HISTORY OF GRASSES AND HERBIVORES

Prior to the Eocene Epoch, no evidence exists for the occurrence either of grasses (Poaceae) or of mammals having teeth adapted to feeding upon them. Primitive ungulates (Condylarths) were widespread during the Paleocene and apparently originated in the Upper Cretaceous (Patterson & Pascual, 1972), but these forms all had low-crowned teeth that lacked complex patterns of enamel. They were almost certainly browsers.

The earliest mammals having hypsodont teeth were the family Archaeohyracidae, of the order Notungulata, that appeared first in the early Eocene strata of Patagonia. They were followed in the middle Eocene by the Notohippidae, belonging to the same order. In the latter family, the evolution of hooflike feet was superficially similar to the much later evolution of hoofs in North American horses. Careful analyses of the land-borne sediments in which these remains were found makes highly probable the conclusion that the animals lived in open savannas, dotted with trees and shrubs, having an aspect not unlike that of the pampas of temperate South America when first visited by Europeans (Andreis, 1972; Spaletti & Mazzoni, 1978). In these strata opalines that were derived from epidermal cells of grass leaves, though scarce, were undoubtedly present (Frenguelli, 1930; Teruggi, 1955). Unfortunately, their state of preservation is such that they cannot be identified as to subfamily or tribe. Contemporary Eocene strata of North America contain fossils of herbivorous mammals, including Condylarths

and primitive ungulates, but these all have characteristics associated with browsing rather than grazing.

The origin of both these Eocene grasses and grazers of temperate South America is in doubt. The Notungulates may have evolved from the more primitive Condylarths that are found abundantly in Paleocene strata, in response to selective pressures produced by the changing habitats. Could the grasses have also evolved from more primitive, forest-loving groups? This hypothesis is certainly plausible, in view of the present distribution of primitive grasses in the forests of tropical South America. This region is a center of diversity not only for bambusoid grasses having relatively low chromosome numbers, (Soderstrom & Calderón, 1974), but also for genera such as *Streptochaeta* and *Anomochloa*, that are either archaic or appear to have diverged in their own unusual direction from primitive ancestors.

One cannot, however, conclude from these facts that the Gramineae as a whole originated in South America. Bambuseae having similar low chromosome numbers exist also in West Africa, and the subfamilies of nonbambusoid grasses that had the largest number of unspecialized characteristics, particularly the Arundinoideae, tribe Danthonieae, are far better developed in Africa than in South America. Furthermore, the isolation of South America during the Eocene would make highly improbable the emigration of Poaceae from that continent to the other continents where they certainly existed during the middle of the Tertiary Period. The existence of the subfamily Oryzoideae in Europe during the Upper Eocene (Litke, 1968) is highly significant in this connnection. Consequently, I believe that Poaceae most probably entered South America from the Old World, possibly Africa, during the Paleocene Epoch or the uppermost Cretaceous. Although Africa and South America were already well separated during this time, islands may well have existed between them in the South Atlantic. These could have served as stepping stones for long distance migration. This hypothesis has been advanced by Raven & Axelrod (1975) for many elements of the South American biota, both flora and fauna.

During the Oligocene, the coevolution of grasses and herbivorous grazers in South America continued along the lines that were begun during the Eocene. Several groups of Notungulates became even more diversified and specialized for life in open savannas. The accompanying evolution of grasses has left no record, except that the scattered presence of opaline siliceous bodies suggests that they also were actively evolving. In North America, the earliest evidence that Poaceae were present comes from the Florissant deposits of uppermost Eocene or earliest Oligocene (MacGinitie, 1953; Beetle, 1958; see Epis & Chapin 1975 for accurate dating). These are fruits of two different kinds, one of them belonging to the tribe Stipeae, and perhaps the genus *Stipa* itself, and the other possibly to the genus *Phalaris*. Both of these genera belong to the subfamily Pooideae, but to different tribes, Stipeae and Phalarideae, respectively. The existence of such genera, that are end branches of different lines of evolution within the subfamily, suggests that the Pooideae were already well differentiated at that time. This conclusion agrees well with the completely modern character of the pooid fragments of epidermis found by Litke (1968) in Miocene coal-bearing strata of Germany.

Both *Stipa* and *Phalaris* most probably reached North America from Eurasia.

The probable origin of subfamily Pooideae ("Festucoideae") in temperate Eurasia has been emphasized by Hartley (1973) on the basis of modern distribution patterns. The two largest genera of the tribe Stipeae, *Stipa* and *Oryzopsis*, both have pronounced centers of diversity in central Asia (Komarov, 1934). The species of (*Phalaris*) are also primarily Eurasian. Consequently, the earliest known grasses that inhabited open savannas in North America appear to have acquired their distinctive characteristics by a course of evolution that took place during the Eocene Epoch in Eurasia.

Even though temperate South America is at present a center of diversity for the tribe Stipeae, it probably was not the center of origin for the tribe. The paleosoils of Eocene and Oligocene age in temperate South America, including those of the temperate pampas where Stipeae are now abundant, have been examined as carefully as have the Miocene deposits of North America. The absence of stipoid fossils from South American deposits is, therefore, as significant as their abundance in North America. Stipoid grasses most probably migrated from North to South America contemporaneously with the ungulates of North American origin, such as camels and horses.

Incredibly rich deposits of stipoid fruits of "seeds" have been found in Miocene and Pliocene deposits of central North America, extending from Nebraska and Kansas west to Colorado, and southward to New Mexico. They provide what is probably the best fossil sequence of herbaceous angiosperms anywhere in the world. Even though the stratigraphic succession, as worked out by Elias and others, has recently been questioned (Thomasson, 1979), a phylogenetic succession of fruit forms can still be recognized. The known sequence begins in the early to middle Miocene with *Berriochloa primaeva* Elias, which apparently has no modern counterpart, and ends in the Lower Pliocene with a series of well-differentiated forms that can be assigned to the modern genera *Stipa*, *Oryzopsis*, *Piptochaetium* and *Nassella*.

Stipoid grasses evolved contemporaneously with two groups of grazing ungulates, horses and pronghorn "antelopes." The Eocene and Oligocene representatives of the horse line that evolved in central North America were small to medium-sized in stature, had low-crowned teeth and feet consisting of three or more digits (Romer, 1966; Simpson, 1951). During the Miocene, successive genera of horses increased considerably in size. At the same time, they radiated adaptively into two different lines. One of them led to *Anchitherium* and *Hypohippus*, which became relatively large, but retained teeth equipped for browsing (Simpson, 1951). In the other, represented in the Miocene by *Merychippus*, adaptation to grazing evolved through the acquisition of teeth having more complex patterns of enamel, accompanied by cement. These horses also ran more firmly on their middle toe and acquired a springing gait more like that of modern horses. In the earlier horses and the *Anchitherium-Hypohippus* line, the hind part of the foot consisted of a flexible pad or cushion, much as in the feet of modern dogs or camels. The presence of this pad prevented the animal from flexing its toes or hoofs, an action of horses that is essential for fast running of a relatively large animal. Consequently, an adaptive change correlated with the altered teeth was the loss of this pad, and the evolution of a springing motion during running, based upon the flexion of the middle toe. *Merychippus* and its descendants became

adapted to more open savannas, that were increasing in extent during the Miocene epoch. The shift in diet was probably a result of selective pressure brought about both by the increased abundance of grasses relative to the foliage of shrubs and trees, and intense competition for the latter from other browsers including tapirs, rhinoceroses, chalicotheres and camels, as well as *Anchitherium*-type horses. The perfection of teeth adapted for grazing most probably coincided with the evolution of firmer, more siliceous leaves on the part of the grasses that grew in the more open areas.

At the end of the Miocene, a second adaptive radiation took place. Three closely related lines of this radiation retained the three-toed hoofs of *Merychippus*, but acquired teeth having higher crowns. The three terminal forms, *Nanippus*, *Neohipparion* and *Hipparion*, differed from each other in body size and details of tooth structure. Of these, *Nanippus* and *Hipparion* persisted throughout the Pliocene. In the fourth line, represented during the Pliocene by *Pliohippus* and later by modern horses (*Equus*), the changes in teeth were somewhat similar, but those of legs and toes were more profound. The legs became longer and more slender, and the side toes were lost, producing the single large hoof characteristic of modern horses.

A highly significant fact about Pliocene evolution of horses, worked out in detail for the Great Basin by Shotwell (1961), was the contemporaneous and largely sympatric existence of two quite different kinds of horses, *Hipparion* and *Pliohippus*. Shotwell infers that they occupied somewhat different habitats; *Hipparion* living in savannas or parklands containing many trees and shrubs, while *Pliohippus* occupied the more open areas. He suggests that the side toes provided added traction in dodging movements while the animal was escaping from predators in savannas or parkland, while the presence of a single large toe made running in a straight line more efficient for a horse that lived chiefly or entirely in open country. Comparing the distribution throughout the Pliocene of *Hipparion* and *Pliohippus*, Shotwell concludes that the spread of *Pliohippus* at the expense of *Hipparion* coincided closely with spread of open grassland, replacing savanna or parkland. Apparently, the direct response to the increasingly dry climate was with respect to the flora, but that the horses, with little or no further evolution, altered their distribution in response to the change in vegetation. Thomasson, reviewing the change in vegetation and in horse distribution in the Great Plains of the central states, concludes that the same interacting succession of events took place there.

Unfortunately, grass fruits have not been found in deposits younger than early Pliocene, so that the changes in flora during the last five million years cannot be followed. The changes that took place must be inferred from comparisons between the fossil fruits dating from the earliest Pliocene and the composition of the modern floras. These are as follows. In the South American pampas the stipoid genera *Stipa*, *Nassella* and *Piptochaetium*, not known as fossils, are now abundant and represented by a large number of species. In North America, on the other hand, stipoid grasses are much less abundant than they were during the early Pliocene. The genus *Stipa* is represented chiefly by *S. comata*, *S. spartea*, *S. viridula* and *S. robusta*, all of which have fruits that differ considerably from the Pliocene fossils. A fact to be noted is that the first three of these species are

polyploids. The chromosome number of both *S. comata* and *S. spartea* is $2n = 44$ to 46, depending upon the presence or absence of a small extra pair, perhaps of B-type chromosomes (Stebbins & Love, 1941). That of *S. viridula* is $2n = 82$ (Johnson & Rogler, 1943). Since the modern fruits of these species are considerably larger than any of the Pliocene fossils, one can suspect that their polyploidy arose during the later Pliocene, Pleistocene, or even more recently.

The other two genera that are known from fossils of Pliocene age, *Nassella* and *Piptochaetium*, are now absent from the central and western grasslands. *Piptochaetium* survives in the arid mountains of the southwest, as well as in the form of two species that are usually placed in the genus *Stipa*, *S. avenacea*, which occurs in rocky woods throughout the eastern United States, and *S. avenacoides*, native to open, savannalike woodlands in Florida. North of temperate South America, *Nassella* is represented only by a few localized species in Mexico and Central America.

The stipoid grasses have been largely replaced in the Great Plains by genera belonging to three completely different tribes; the bluestems (*Andropogon*, s.l.), belonging to the tribe Andropogoneae; switchgrass (*Panicum virgatum*), tribe Paniceae; grama grass (*Bouteloua curtipendula* and *B. gracilis*) and buffalo grass (*Buchloe dactyloides*), the latter two both of the tribe Chlorideae. When and why did this revolutionary change take place?

No definite answer can be given to either of these questions. The answer to the question "when?" is made difficult by the absence of grass fossils dating from the Upper Pliocene and Pleistocene epochs. If, as seems likely, stipoid grasses were associated chiefly with savannas and grasses belonging to other tribes were predominant on open plains, then the gradual restriction of savanna habitats, as can be inferred from the distribution of *Hipparion* and other fossil mammals, must have been associated with a similar decrease in abundance of stipoids, or at least of those species that occur in the early Pliocene deposits. This would mean that by the end of the Pliocene epoch, the genera *Berriochloa*, *Piptochaetium* and *Nassella* had already disappeared from most of the central plains. Nevertheless, they probably persisted in some parts of the area as late as early Pleistocene. This inference is based upon my belief that their invasion of the South American pampas was simultaneous with the transcontinental migration of northern ungulates, particularly horses (Equidae) and Camelidae. This migration is usually dated as immediately following the appearance of the Panamanian land bridge, at the end of the Pliocene or the beginning of the Pleistocene epoch.

At the beginning of the Pleistocene glaciations, therefore, the composition of the grass flora of the central plains was probably already different from that recorded in lower Pliocene deposits. Such a change would be expected as a result of increasing aridity and progressively colder winters, which is evident from the composition of woody floras from throughout the western United States (Axelrod, 1975). Species of the genera *Stipa* and *Oryzopsis* were probably there, as they are today, as well as *Agropyron* and *Elymus*, which probably entered North America from Eurasia during the Pliocene (Stebbins, 1974). Species of the genus *Panicum*, perhaps descendants of the Mio-Pliocene *P. elegans* and relatives of the modern *P. virgatum*, were probably present. Nevertheless, good reasons exist for believing that three of the dominant elements of the modern grass flora,

the bluestems (*Andropogon* or *Schizachyrium*), indian grass (*Sorghastrum*), grama grasses (*Bouteloua*) and buffalo grass (*Buchloe*), were either absent or uncommon. As discussed elsewhere (Stebbins, 1974) the species of these groups that now dominate the plains are polyploids that appear to have close diploid relatives either in the southern United States or in Mexico. The polyploid complexes to which they belong have distribution patterns that suggest youthfulness (Stebbins, 1971). I believe, therefore, that these species are of post-Pleistocene origin.

Throughout the Pliocene epoch, the mammalian herbivores that dominated the Great Plains belonged to the same evolutionary lines that had been evolving there during the Miocene: horses, pronghorn "antelopes" and camels. They were becoming larger, and gave rise to a number of branches off their main evolutionary lines. Nevertheless, their effect upon the plains grasses must have been similar to that exerted by their Miocene ancestors, though perhaps more intense.

The Pleistocene glaciations, plus the profound effects that they exerted on both climate and soil for hundreds of miles south of the ice margin itself, must have altered greatly the central and western grasslands. Immediately south of the ice margin, grasslands were replaced by tundra and spruce forest, even in areas that are now short grass plains, such as north and central Nebraska (Davis, 1976). During drier periods, the accumulation of loess must have altered greatly soil conditions, contributing further to the displacement of floras.

During the Pleistocene epoch, the fauna of herbivores was altered by the arrival of bison and sheep from Eurasia. These animals graze more closely and densely than do horses and pronghorns, which dominated the plains before their arrival. They would be particularly destructive to long-leaved caespitose or bunch grasses, such as most species of *Stipa* and perennial Triticeae. On the other hand, rhizomatous, sod-forming grasses, such as *Bouteloua* and *Buchloe*, would be much more resistant to their grazing pressure.

For these reasons, I believe that the grassland vegetation of the central and western United States, as recorded by the botanists who first visited the area during the nineteenth century, consists of recent plant communities that were put together after the retreat of the last ice sheet. Some of their contemporary species may have arrived or at least spread during comparatively modern times, as a result of burning and other activities on the part of the Indians (Gleason & Cronquist, 1964: 206–208). Coevolution of grasses and herbivores has progressed continuously on the North American grasslands ever since they first appeared as savannalike openings in the forest during the early part of the Tertiary period.

CONCLUSION

In spite of large gaps in the fossil record, available information permits a partial synthesis that reveals close connections between the evolution of large mammalian grazing herbivores and the grasses upon which they fed. This coevolution began during the Eocene Epoch, 45 to 55 million years ago, and has continued up to the present. Further research studies, conducted in a variety of disciplines, will surely fill in and amplify the picture. Paleosoils need to be examined more carefully, with particular reference to the possible occurrence in

them of opaline silica bodies derived from grass leaves. Whenever these are well enough preserved, they could be examined by agrostologists who might be able to determine at least approximately their systematic affinities. More information is needed about the stipoid fruits found in the Great Plains area, particularly their total distribution in both space and time. At the same time, careful morphological comparisons between the fruits of species belonging to modern stipoid genera will help greatly in the classification of the fossil forms, and for estimating the amounts of difference between them. A synopsis of morphological and histological characteristics of stipoid fruits on a worldwide basis will be necessary for interpreting such comparisons. Cytogenetic and biochemical comparisons of different modern species and genera will be a necessary prelude to the interpretation of evolutionary relationships.

In addition, the effects of grazing animals upon the species composition need to be better understood. Research workers in the discipline of range management have conducted many experiments to show that different intensities of grazing affect greatly the species composition of range lands. In addition, trampling by hoofs of the grazers exerts additional effects, particularly during wet seasons. This kind of damage is quite different depending upon the kinds of hoofs that the different species of grazers possess. Other factors are the different sizes of the flocks and herds that are characteristic of different species, and the tendency of some of them to travel long distances, while others remain for relatively long periods of time in the same area. I am not aware of any careful investigations even of the comparative effect on range lands of different kinds of modern domestic animals, such as horses and cattle, although ranchers and range specialists are well aware of the existence of differences, and anecdotal accounts of them are numerous. In this entire field, the opportunities for collaborative research are very great. They can be directed toward a highly valuable aim: interpreting the evolution of two of the world's major food resources—grasslands and grazing animals. Mankind has depended upon them for his existence ever since our remote ancestors ventured onto the savannas and began a new mode of existence.

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